Tardigrades of the Australian Antarctic Territories: the Northern Prince Charles Mountains, East Antarctica

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During the austral summer of 1990–91, a survey of Tardigrada inhabiting terrestrial mosses and lichens was conducted in the northern Prince Charles Mountains, East Antarctica. Five genera and six species were recovered including *Echiniscus jenningsi*, *Diphascon sanae*, *Hypsibius antarcticus*, *Macrobiotus blocki*, *Macrobiotus stuckenbergi*, *and Milnesium tardigradum*. A model is proposed for the dispersal of tardigrades to and within East Antarctica. Cryptobiotic tardigrade tuns are carried aloft and over Antarctica via upper air currents, then descend over the centre of the continent and radiate outward to peripheral areas on katabatic winds. The deflection of surface winds by Coriolis forces allows for east to west dispersal from established populations along the East Antarctic Coast. Males have seldom been reported in the genus *Echiniscus*, but 30% of the *E. jenningsi* found were male. The strategy of sexual reproduction is discussed relative to distributional and survival challenges of tardigrades in East Antarctica.

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INTRODUCTION

The presence of tardigrades in Antarctica has been known for most of the twentieth century. Richters (1904) reported the first tardigrades from East Antarctica on the Wilhelm II Coast (see review by Miller et al. 1988), but the makeup of the fauna and the distribution of the member species is only beginning to emerge. There are no previous records of tardigrades from the northern Prince Charles Mountains although the animals have been reported from other East Antarctic locations. West of the Prince Charles Mountains, tardigrades have been recorded from Robertskollen (Ryan et al. 1989, Dastych et al. 1990, Dastych and Harris 1994), the Prince Olav Coast near the Japanese station at Syowa (Morikawa 1962; Sudzuki 1964, 1979; Sudzuki and Shimoizumi 1967; Utsugi and Ohyama 1989), Enderby Land around the Russian base at Molodezhnaya (Opalinski 1972, Dastych 1984, Utsugi and Ohyama 1991), and along the Mawson Coast (Miller and Heatwole 1995). To the east, tardigrades have been collected in the Larsemann Hills (Miller et al., 1994a), the Vestfold Hills near the Australian research base of Davis (Everitt 1981, Miller et al. 1988), the Wilhelm II Coast (Richters 1904, 1907), the Bungar Hills (Korotkevich 1964), and the Windmill Islands around the Australian research station at Casey (Thomas 1965; Dastych 1989; Miller et al. 1994b, 1996).

Continental Antarctica has a few truly terrestrial ecosystems. Mosses, lichens and a few algae persist in the harsh conditions (Filson 1966). These plants are widely scattered

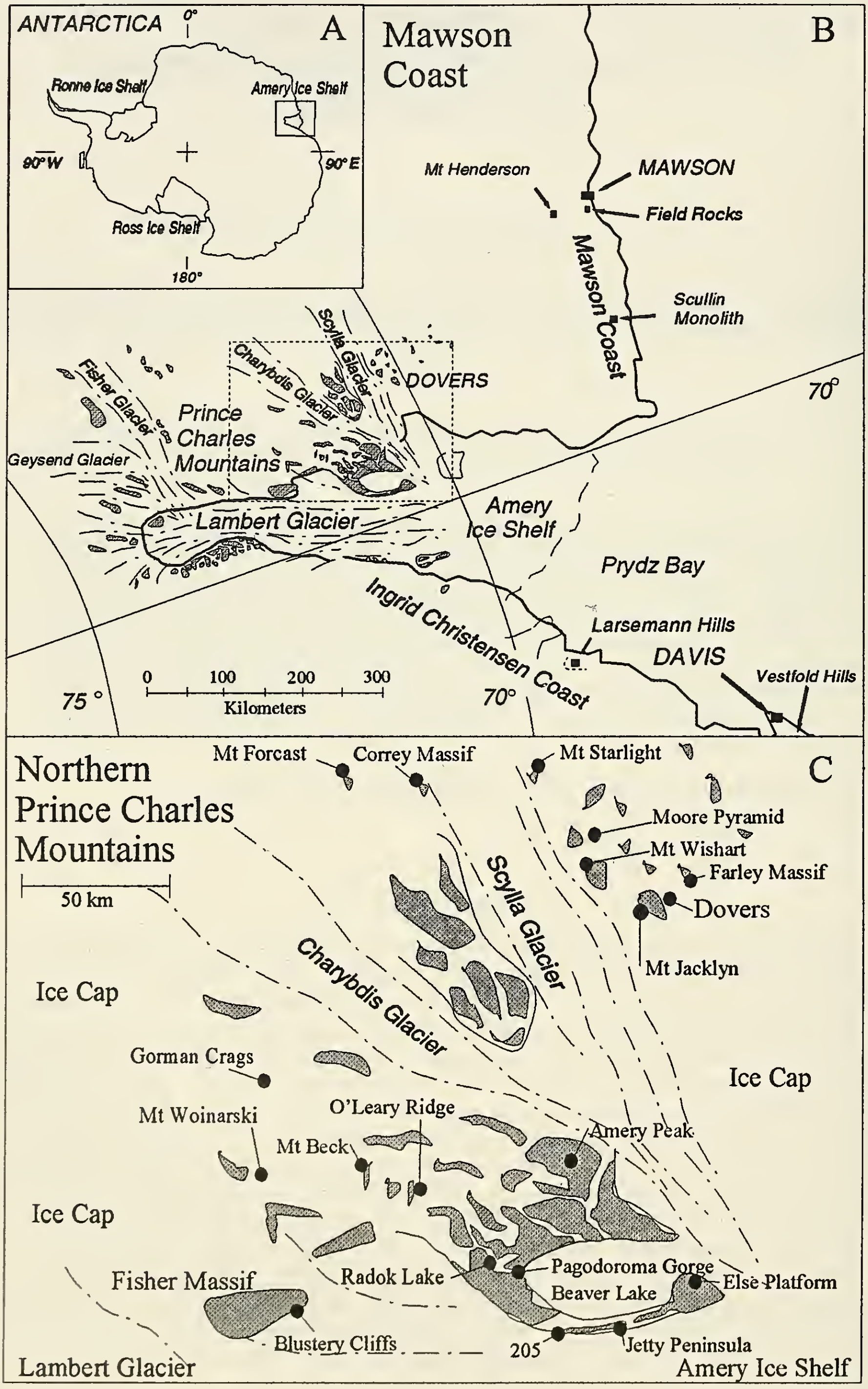

Fig. 1. Location maps of: A, Antarctica; B, Mawson Coast, Amery Ice Shelf, Lambert Glacier, and the Prince Charles Mountains; C, Northern Prince Charles Mountains showing study areas.

over the small areas of unfrozen land that ring the edge of the continent or protrude through the ice as nunataks. Heatwole (1983) and Heatwole et al. (1989) characterised the bacteria, yeasts, fungi, unicellular algae, rotifers, nematodes, tardigrades, and mites that inhabit the mosses, lichens, and rudimentary polar soils. The present paper treats the phylum Tardigrada from the Prince Charles Mountains, East Antarctica.

STUDY AREA

The northern Prince Charles Mountains, East Antarctica, consist of hundreds of nunataks and several large massifs located on the continental ice cap at the western edge of the Lambert Glacier and south of the Amery Ice Shelf (Figs. 1A, 1B). They extend 500 km to the south of Dovers, a temporary Australian Antarctic research camp on the north edge of the range. Dovers is on the ice cap (Fig. 1 C), 1500 m above sea level on the edge of the Scylla Glacier about 500 km west of the Australian station of Davis and 300 km south of Mawson station, at 70° 36' South and 66° 50' East (Fig. 1B). The Dovers camp was inhabited only during the austral summers of 1989–90 and 1990–91.

These mountains consist mainly of Precambrian basement rocks of the extensive East Antarctic Shield (Trail and McLeod 1965, Tingey 1982, James and Tingey 1983, Fitzsimons and Thost 1992), protruding above the ice cap at elevations mostly of 1000–2000 m above sea level (actual collecting sites 830–2160 m). However, three areas of importance to the present study, Jetty Peninsula, Else Platform, and Pagodroma Gorge, differed by being located at lower elevations (sea level-215 m) in the Beaver Lake garden, an area of downfaulted Permian to Early Triassic strata of sandstones and subordinate conglomerates, siltstones, shales, and coal (Mond 1972, McKelvey and Stephenson 1990).

The study area included 17 localities encompassed by the coordinates: 70° to 72°S; 65° to 70°E (Table 1; Figs. 1B, 1C). Of those, 13 did not yield tardigrades and are not described here, except to note that all but one (Else Platform) were nunataks at higher elevations where lower temperatures, higher winds, and more desiccation prevailed than at lowland sites. The upland sites either lacked lichens and/or mosses, or had them represented only as small widely scattered clumps or encrustations in sheltered rock-crevices. In some cases, several days of intensive search yielded only 1–3 thalli or cushions, all less than 1 cm in diameter.

Blustery Cliffs is located on the northern end of the Fisher Massif. The site consists of a flat, granite plateau bordered by steep rock slopes (Fig. 2A) that level off at the base into a scree slope and then another rocky plain. The plateau is partly covered by shallow drift snow up to 50 cm deep, from which boulders protrude. There are occasional patches of bare soil (up to 1 m in diameter) exposed between rocks, as well as more extensive areas swept bare of snow. The gray-brown soil is up to 3 cm deep and consists of small gravels with some pebbles and cobbles on top. On warm days snow melts and conditions are moist until re-freezing occurs. In places the surface 1–2 cm of soil dries out. The lower plain is similar except that the soil is deeper (15 cm) and boulder beds are interspersed with snow banks. Basal slopes are of jumbled boulders with only occasional, small pockets of soil about 20 cm in maximum diameter.

A few mosses occur only as small, widely scattered cushions 1 cm or less in diameter, located on moist soil either in sheltered rock-crevices on the cliff face, or between boulders on the plains. There are at least three species of lichens, all occurring as crustose thalli up to 5 cm in diameter (Fig. 3A). They grow on rock in crevices on the cliff face or on sheltered surfaces of boulders on the plain or scree slope.

Jetty Peninsula is a thin strip of exposed land (Fig. 2B) extending 60 km south of Else Platform and separating the frozen Beaver Lake from the Lambert Glacier. It consists of highly weathered sandstone, broken into frost polygons usually 20 cm or less in diameter. The substrate is of sand strewn with pebbles, cobbles, and occasional large boulders. There are local areas of flat rock. Scattered patches of snow supply meltwater. The soil is usually 3–13 cm deep and is moist, or if dry, only in the top centimetre.

This was the most highly vegetated area visited. Cushions of mosses grow where boulders shelter the ground. Lichens encrust on small stones in the furrows between polygons, on the northern faces of large boulders (Fig. 3B), and occasionally on flat rock in the open. There were at least four species of lichens and one of mosses.

Amery Peak rises west of the Loewe and Manning Massifs between Dovers base camp and the Jetting Peninsula. This area was visited by Dr Chris Fielding, who donated a moss specimen described as moss collected growing on the ground on the northeastern side of the Peak.

Radok Lake is fed by the Bathye Glacier and drains via Pagodroma Gorge into Beaver Lake. A single moss-covered soil sample collected by Dr Don Adamson in early 1989, and donated by Ms Penelope Greenslade, contained tardigrades.

TABLE 1.

Collection localities in the Prince Charles Mountains.

Locality	Altitude	Mosses	Lichens	Dates
		Tardigrades found		
Blustery Cliffs	830–1135	Yes	Yes	20-21 Jan, 1990
Jetty Peninsula		Yes	Yes	25-26 Jan, 1990
Amery Peak		Yes**	—	Early 1990
Radok Lake		Yes**	—	Early 1990
		Tardigrades not found		
Mt Woinarski	1100–1560	No	No	13-18 Jan, 1990
Pagodroma Gorge	215	No	Yes	22-24 Jan, 1990
Else Platform		Yes	Yes	28Jan, 1990
Mt Wishart	1300–1670	Yes*	Yes*	Jan-l Feb, 1990
Moore Pyramid	1900–2160	No	Yes*	3-4Jan, 1990
Mt Starlight	2150	No	No	6 Feb, 1990
Mt Forcast		Yes	Yes	9Feb, 1990
Correy Massif	2060	No	Yes	10-11 Feb, 1990
Mt Jacklyn		No	Yes	13 Feb,1990
Farley Massif		No	Yes	16 Feb, 1990
O'Leary Ridge		—	Yes**	—
Mt Beck		—	Yes**	—
Gorman Crags		—	Yes	—

* Only 1–3 small samples, each less than 1 cm found in area
** Not visited by authors, samples donated by other expeditioners
— Data not avaliable

METHODS

Field work was carried out by the junior author in January and February 1990 with logistical support from Dovers base camp. It served as a helicopter base from which expeditioners were distributed in pairs to distant localities where they set up a tent and carried out their research. Field work at each locality was conducted on foot; all available habitats were searched for mosses and lichens. At each sampling site, lichens were scraped from rocks with a knife and either entire moss cushions or 25 mm diameter cores

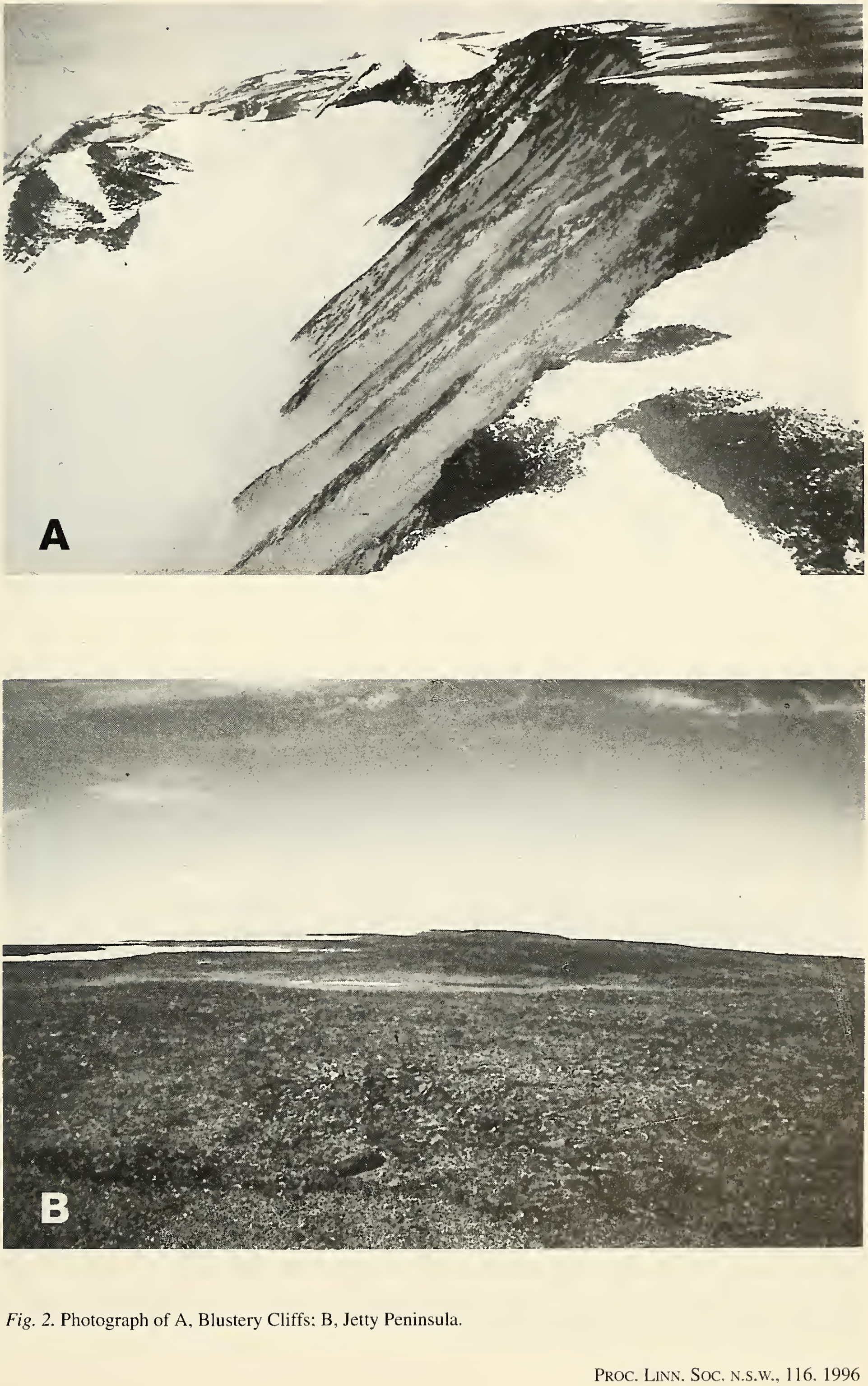

Fig. 2. Photograph of A, Blustery Cliffs; B, Jetty Peninsula.

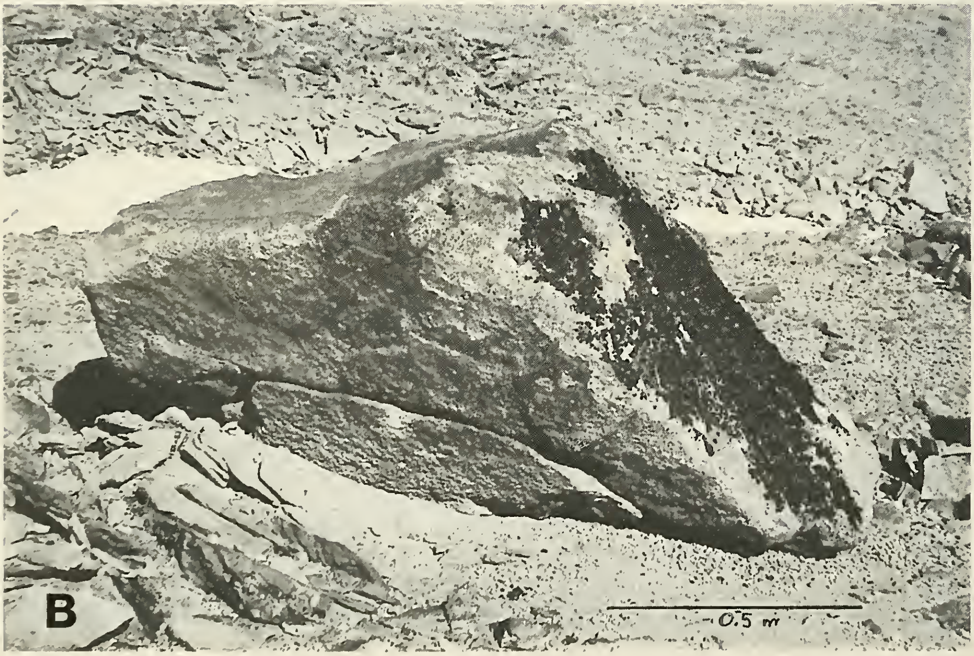

Fig. 3. Photograph of lichens at A, Blustery Cliffs; B, Jetty Peninsula

were taken. All samples were frozen and returned to Australia for extraction of animals. Fourteen moss and 46 lichen samples were obtained.

Extraction of animals was carried out by soaking the moss or lichen for 48 hours in a 4% sucrose solution with a drop of sodium pentobarbitone additive. Several washings, during which the plant was squeezed, were filtered through a 63-micrometer nylon mesh to strain out finer material. The debris was preserved in 5% buffered formalin. Later the tardigrades were separated under a dissecting microscope. Individual animals were transferred to slides with an Irwin Loop, mounted in iodine enhanced Hoyer's medium, capped with a glass coverslip and sealed by epoxy paint.

Identification of tardigrades was established using a phase-contrast microscope. The microscopic image was captured with a CCD video camera and a personal computer to produce video-micrographs. The image was printed by laser printer and used for measurements and drawings.

The works of Homing et al. (1978), Schuster et al. (1980), Ramazzotti and Maucci (1983) and Dastych (1984) were used for primary identification. Taxonomic criteria and terminology follows Ramazzotti and Maucci (1983), except as noted. Representative specimens were deposited at the Australian National Insect Collection, CSIRO Division of Entomology, Canberra, ACT, Australia and in the Zoological Museum, Hamburg.

RESULTS

From the 725 tardigrades collected, five genera and six species were identified. There were 369 (50.9%) specimens identified as *Hypsibius antarcticus* (Richters 1904), 276 (38.1%) as *Macrobiotus blocki* Dastych 1984, 46 (6.3%) as *Echiniscus jenningsi* Dastych 1984, 20 (2.8%) as *Macrobiotus stuckenbergi* Dastych, Ryan, and Watkins 1990, 13 (1.8%) as *Milnesium tardigradum* Doyere 1840, and one (0.1%) as *Diphascon sanae* Dastych, Ryan, and Watkins 1990 (Table 2). Each species conforms to the descriptions reported by the same authors from the Mawson Coast (Miller and Heatwole 1995).

Of the 60 samples (1 soil, 14 mosses, and 45 lichens) collected, only 14 (23%) contained tardigrades. Representation by species within the positive samples was not uniform. *Macrobiotus blocki* was found in 10 (71%) of the 14 positive samples and *Macrobiotus stuckenbergi* in five (35.7%). Less frequent were *Echiniscus jenningsi* which occurred in four of 14 (28.6%) and *Milnesium tardigradum* which was found in three (21.4%). The least frequent were *Hypsibius antarcticus,* present in only two of 14 (14.3%) and *Diphascon sanae,* present in only one (7.1%).

Species occurrence at any positive site was low. Only one of 14 sites (7.1%) yielded four of the six species and two sites (14.3%) had three. Eleven of the positive samples (78.6%) had two species or less. Different mixtures of genera and species were found at different collection sites. Table 2 details the number of animals found at each site and shows the co-occurrences of the species. The collections at Blustery Cliffs contained five of the six species of the collective tardigrade fauna. The collections along Jetty Peninsula yielded four of the six species. Only one species was recovered from Amery Peak and Radok Lake.

DISCUSSION

The nunataks and massifs of the northern Prince Charles Mountains are free of ice in summer and are not unlike islands in a sea (Miller et al. 1988). The water around them may be frozen but the problems of dispersal and survival for plants and animals are as real as for any island. Mosses and lichens were first collected from the Prince Charles Mountains of MacRobertson Land in 1962 (Filson 1966). Even under the harsh environ-

TABLE 2.

Species and numbers of tardigrades collected from various habitats in the Prince Charles Mountains.

Site	Localities	Habitat	*Echiniscus jenningsi*	*Diphascon sanae*	*Hypsibius antarcticus*	*Macrobiotus blocki*	*Macrobiotus stuckenbergi*	*Milnesium tardigradum*
1	Blustery Cliffs	Moss				28		
2	Blustery Cliffs	Moss	1			5		
3	Blustery Cliffs	Lichen				1		
4	Blustery Cliffs	Lichen			368		1	
5	Blustery Cliffs	Soil		1	1		6	
6	Jetty 205	Lichen				1	1	
7	Jetty 205	Lichen	1					1
8	Jetty Peninsula	Moss	43			3	1	7
9	Jetty Peninsula	Moss				3		
10	Jetty Peninsula	Moss	1			58	11	
11	Jetty Peninsula	Lichen				28		5
12	Jetty Peninsula	Lichen				2		
13	Amery Peak	Moss				107		
14	Radok Lake	Moss				40		
Total:		**725**	**46**	**1**	**369**	**276**	**20**	**13**

mental conditions found along the Lambert Glacier and the Amery Ice Shelf, tardigrades were expected to be found because the phylum is known to survive greater extremes than exist naturally (Crowe 1972).

When subjected to adverse conditions, many tardigrade species enter a deeply dormant state, known as cryptobiosis, a reversible suspension of metabolism (Clegg 1973, Crowe 1975, Kinchin 1994, Wright et al. 1992). When cryptobiotic, tardigrades shrivel into a tun and can tolerate experimental extremes such as lack of moisture, strong vacuums, ionising radiation, noxious chemicals, high heat, and cold approaching absolute zero (Ramazzotti and Maucci 1983). Tardigrades have remained viable in the cryptobiotic state for over a century (Franceschi 1948, Kinchin 1994). Clearly, tardigrades have the capacity to sustain life for long periods of time, through the rigours of long distance dispersal, and within a hostile environment upon reaching a destination.

Logs of distant origin have been reported as washing up on Subantarctic Heard and Macquarie Islands (Smith et al. 1989). However, none were reported to contain lichens or mosses and it is likely that tardigrades, along with their habitat, usually would be washed off such flotsam well before arriving in polar regions. No wood has been reported on continental Antarctic shores. Thus, sea dispersal of tardigrades to Antarctica via flotsam seems unlikely, or at best rare, and in any event could not account for range extensions from the coast to interior locations like the Prince Charles Mountains.

Birds regularly fly between the Antarctic and distant regions and could transport tardigrades either in mud on their feet, or perhaps in their feathers. Most are sea birds and periodically settle on the water and would have their legs rinsed of any mud. Furthermore, even after arrival few stray very far into the interior. Three species of birds have been recorded from the northern Prince Charles Mountains, the Snow Petrel *(Pagodroma nivea),* the South Polar Skua *(Catharacta maccormicki),* and Wilson's Storm Petrel *(Oceanites oceanicus)* (Heatwole et al. 1991). The last has only been noted as an accidental visitor, but the former two nest there, although in only a few localities. The Snow Petrel nests in crevices in cliffs and along boulders, habitats that are occupied by mosses and lichens (see Study Area above). Even if dislodged in a bare crevice, a tardigrade tun might survive until the arrival and growth of a lichen or moss. The skua nests in the open, but on ground where it could contact moss or lichens. Thus, dispersal via birds, even to areas as remote as the Prince Charles Mountains, is a possibility that cannot be discounted. However, it would appear to be an unlikely event.

Wind seems to be a more probable mode. There are three known wind patterns of relevance. The first consists of easterly, high-altitude winds that circulate from lower latitudes to over the South Pole (Gabler et al. 1990) (Fig. 4A) where it descends in the low pressure trough that exists over the highest, coldest part of the continent as described in the United Kingdom Meteorological Office's Unified Model for the climate of Antarctica (Connolley and Cattle 1994) (Fig. 4B). The second prevailing wind pattern is the katabatic drainage of cold air from the Polar Plateau toward the periphery (Connolley and Cattle 1994, Rubin 1965) (Figs. 4B, C). These winds are often of high velocity and would blow straight north except for the easterly rotation of the earth that bends them in a counterclockwise direction around the South Pole, the Coriolis effect (Fig. 4C). Finally, there are eddies and local winds of a temporary character that can shift direction but generally flow counterclockwise and parallel to the coast (Fig. 4C).

A model of tardigrade dispersal to, and within, East Antarctica is now proposed that is consistent with these wind patterns. It is suggested that on other continents, tardigrade tuns are blown airborne with dust and other debris where they are carried aloft, picked up on the upper air easterlies (Figs. 4A, B), and flow toward the south. Over central Antarctica, they descend over the eastern Polar Plateau, drawn into the polar trough of low pressure, and from there are dispersed peripherally by the surface level, katabatic wind drainage (Figs. 4B, C). Coriolis deflection and the shape of the Antarctic land mass, cause these winds and the debris carried with them to be directed laterally along the coast (Fig. 4C).

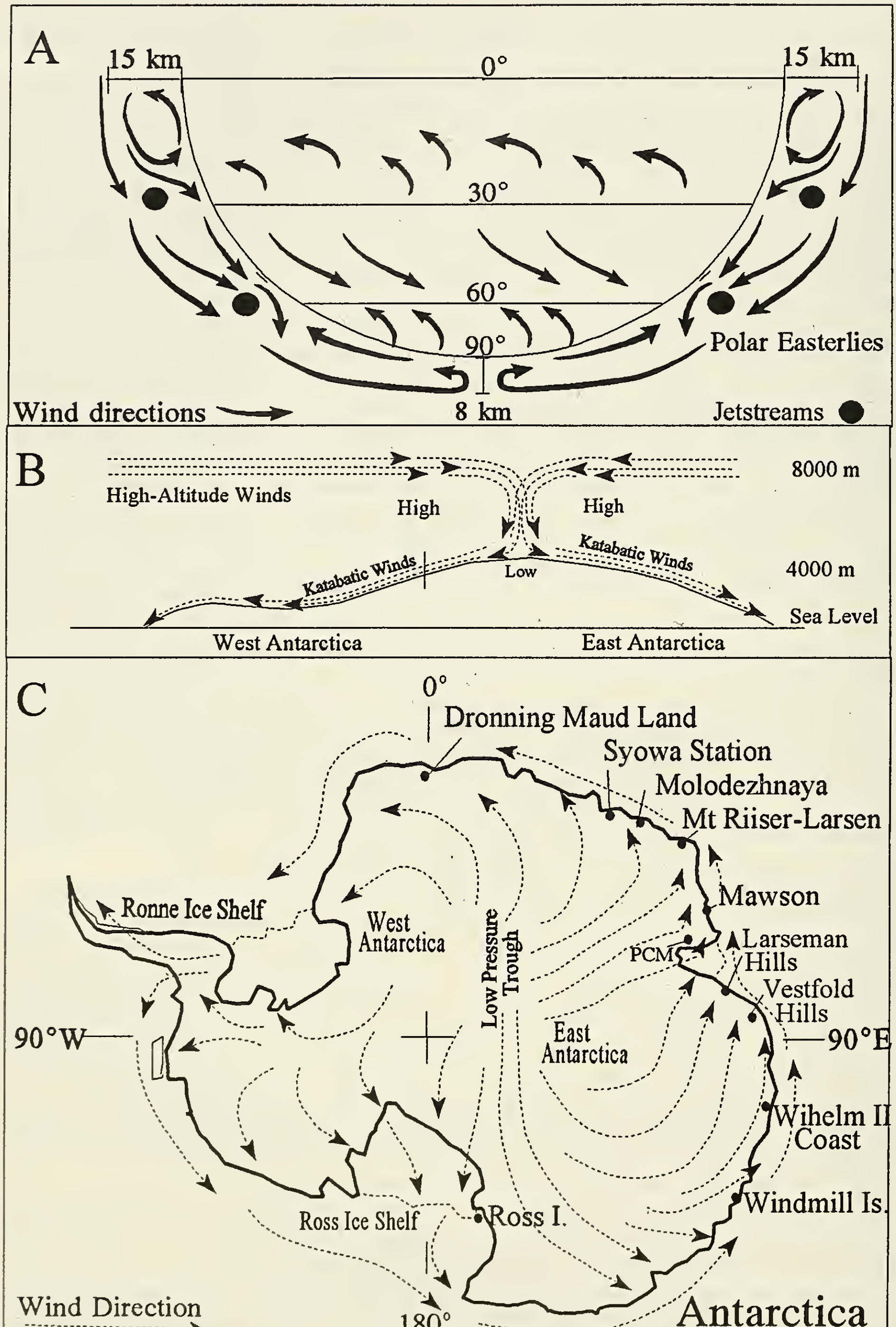

Fig. 4. Model of East Antarctic wind patterns.

The Prince Charles Mountains may have two external sources of tardigrades. Upper level winds are known to carry small plant propagules and animals much larger and heavier than tardigrade tuns for long distances and even over Antarctica (Gresitt et al. 1960, Clegg 1966). Many tardigrades have very broad, even cosmopolitan ranges, and two of these species, *Milnesium tardigradum* and *Hypsibius antarcticus* (McInnes 1994), were found in this study. The katabatic winds draining off the central ice cap down through the channel of the Lambert Glacier could carry propagules originating beyond the continent and it is likely that cryptobiotic tuns are dispersed to the Prince Charles Mountains in this way. In addition, the counterclockwise movement of the winds could bring propagules from upwind populations on the coast of eastern Antarctica. Once established in the mountains, local populations could serve as foci for further distribution via eddies of episodic winds, or further movement on katabatic winds.

On the basis of dispersal from the coast internally, one would expect that inland locations would be barren in comparison to coastal ones because of the filtering effect of distance on dispersal. In fact, the Prince Charles Mountains and the Mawson Coast have identical species of tardigrades (Miller and Heatwole 1995) and the same number of species as found in the Larsemann Hills (Miller et al. 1994a). There are two probable reasons for this. (1) The present model suggests that dispersal is a combination of centrifugal movement and transit from east to west along the East Antarctic Coast. Under this scenario, the Prince Charles Mountains have the same sources of tardigrade propagules as the Mawson Coast and in terms of distances travelled are marginally closer, rather than farther, from extra continental sources. (2) The long-term tolerance of tardigrades to harsh conditions reduces the effect of distance or time on their capacity to disperse. Indeed, their physiological capabilities might enable them to sustain even the conditions of outer space for a considerable period.

Available habitat “targets” might be a more significant determinant of tardigrade distribution in the Antarctic, these decrease from coast toward the interior. Mosses and lichens are larger and more abundant on ice free areas of the coast as compared to the inland nunataks and massifs, probably because of the harsher climate in the interior. Furthermore, on the coast they sometimes are exposed on open, flat surfaces where the wind can sweep over them, whereas further toward the centre these plants grow mainly in crevices and among rocks where they are sheltered from the wind and, consequently, from access to tardigrade propagules. Despite the Prince Charles Mountains being further inland and with a moss and lichen density much lower and less accessible than on the coast, they have the same species of tardigrades as does the Mawson area (Miller and Heatwole 1995). The determinative role of mosses and lichens in tardigrade distribution would be lessened to the extent that these animals can prosper in other habitats, e.g., Antarctic soils. It should be noted that three species of the present study were extracted from a soil sample.

Although dispersal events are difficult to observe and the proposed model cannot be tested easily, it is a consistent with observed distribution and with wind patterns. It accounts for the presence of cosmopolitan species like *Hypsibius antarcticus* and *Milnesium tardigradum* as well as local endemics. The latter, once established by a rare, chance dispersal and cut off from further significant gene flow, could speciate. Katabatic winds could disperse them to downwind localities on the coast. Local winds would distribute them to adjacent localities. Because of this pattern, East Antarctica may not be an exporter of species.

Table 3 presents the distribution along the East Antarctic coast of the tardigrade species found in the Prince Charles Mountains. All six species are found further downwind but only the two cosmopolitan species have been found upwind. *Hypsibius antarcticus* has a near continuous distribution around the Antarctic continent (Dastych 1991), including all collected upwind locations. This would indicate either a continuous influx from off continent or good lateral distribution or both and wide environmental

TABLE 3.

East Antarctic wind distribution model for tardigrade species collected in the Prince Charles Mountains.

Location	Dronning Maud Land 72S;02W	Syowa Station 69S;39E	Molodez-hnaya 68S;45E	MtRiiser-Larsen & Thala Hills 67S;SIE	Mawson Coast 62S;67E	Prince Charles Mountains 66S;72E	Larsemann Hills 66S;76E	Vestfold Hills 68S;78E	Wilhelm II Coast 66S;9OE	Windmill Islands 66S;110E	Ross Isl & Victoria Land 78S;168E
Reference Code	1	2,3	4	4,5	6	7	8	9,10	11	12,13,14,15	16
Echiniscus jenningsi					← X	X					
Diphascon sanae	← X				X	X					
Hypsibius antarcticus		← X	X	X	X	X	X	X	X	X	X
Macrobiotus blocki				← X	X	X					
Macrobiotus stuckenbergi	← X				X	X					
Milnesium tardigradum		← X	X	X	X	X	X				

Species collected **X** Wind Direction

References

1. Ryan et al. 1989
2. Utsugi & Ohyama 1989
3. Sudzuki 1964
4. Utsugi & Ohyama 1991
5. Dastych 1984
6. Miller & Heatwole 1995
7. This paper
8. Miller et al.1994a
9. Everitt 1981
10. Miller et al. 1988
11. Richters 1904
12. Thomas 1965
13. User & Dastych 1989
14. Miller et al. 1994b
15. Miller et al. 1996
16. Dougherty & Harris 1963

tolerance. *Milnesium tardigradum* is known from a few locations on the Antarctic Peninsula and some of the maritime islands on the other side of the continent (Dastych 1984, Dastych 1989, McInnes and Ellis-Evans 1987, Usher and Dastych 1987), but from only one location directly upwind, the Larsemann Hills (Miller et al. 1994a). This pattern would indicate colonisation from off continent and downwind distribution around part of East Antarctica. We would caution that these patterns may be an artefact of collection and may change as more data becomes available for distributional and ecological analysis.

Three species seem restricted to East Antarctica. *D. sanae* and *M. stuckenbergi* have dispersed around one-quarter of the continent from the Prince Charles Mountains and Mawson Coast to Dronning Maud Land while *M. blocki* has a more limited distribution, being known only from the Prince Charles Mountains, Mawson, and down wind to Enderby Land. These species may have originated in the Prince Charles Mountains and are in the process of being dispersed.

Echiniscus jenningsi is known only from Antarctica. There appears to be two separate concentrations, on opposite sides of the continent. The western concentration is on the Antarctic Peninsula (Dastych 1989, Usher and Dastych 1987) and the maritime islands of the South Shetland Islands (Dastych 1984; Jennings 1976a, 1976b), Signey Island, South Orkney Islands (McInnes and Ellis-Evans 1987). The eastern concentration is along the Mawson Coast (Miller and Heatwole 1995) and the Prince Charles Mountains (this study). We conjecture that *E. jenningsi* developed as a species in the Prince Charles Mountains, has been dispersed counterclockwise downwind around the periphery of the continent to the Antarctic Peninsula, and out along the maritime islands. This distribution follows the wind pattern defined in the model where wind flows around the periphery and outward along the peninsula, not vice versa.

The presence of large, plentiful males is believed by Kristensen (1987) to be a plesiomorphic condition, and as such would indicate that the populations of *E. jenningsi* found on the Mawson Coast and in the Prince Charles Mountains have not evolved far from their ancestral characteristics. Bertolani et al. (1990) suggested that species abundance after dispersal is a function of either a large environmental tolerance or a lower environmental tolerance and parthenogenesis. The finding of amphimictic populations of *E. jenningsi* at widely separated Antarctic locations (Dastych 1987, 1989; Miller and Heatwole 1995) would suggest that for successful long range dispersal, both sexes of *E. jenningsi* must find suitable habitat together. Once established, local dispersion of the species would be realistic because of the increased opportunity for opposite sexes to meet. Between the Mawson Coast collections (Miller and Heatwole 1995) and this report, *E. jenningsi* is reported from moss, lichen, and soil implying tolerance of diverse environments.

The active season in Antarctica is very short, and while a tardigrade could survive a winter or several winters, eventually it must encounter suitable habitat, food, and water and then reproduce. *E. jenningsi* may not have been found at intervening sites because it did not encounter acceptable habitat upon arrival or it may have encountered livable environments but not endured for lack of the opposite sex (Bertolani 1987). By chance, a pair or a gravid female, was carried by the peripheral winds, arrived on the Antarctic Peninsula, survived, reproduced, and further dispersed from there.

This evidence of localised dispersal by an amphimictic species does not conflict with Pilato's (1979) general view that parthenogenesis is an adaptation for successful colonisation by passive dispersal. He and Bertolani (1987) argued that a single parthenogenetic animal reaching an uninhabited but suitable location could establish a population. This probably explains the cosmopolitan distribution of *H. antarcticus* and maybe *M. tardigradum,* although the latter species has discernible sexes and may also reproduce sexually. Two of the six species identified from the Prince Charles Mountains, *M. blocki* and *M. stuckenbergi* are known to have populations with viable eggs at several locations (personal communication, Dr Dastych; and unpublished data, Miller and Heatwole). This is evidence of successful colonisation, but does not demonstrate either sexual or asexual reproduction. Karyological work, such as Bertolani (1982), will be necessary on the Antarctic tardigrades to define whether any of these species reproduce sexually or parthenogenetically.

It would appear that several separate strategies for survival and dispersion are simultaneously in evidence in East Antarctica. Parthenogenetic, cosmopolitan species with wide distributions; bisexual species with limited distribution; and some that are undetermined, can be identified. Dispersal, available habitat, and sexual strategies are, each singly and in combination, limiting factors in East Antarctic tardigrade distribution. Thus, existing tardigrade faunas at any given locality are those that have arrived, reproduced, and survived over time and this process may still be occurring.

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